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The structure and function of the vegetative mycelium of mycorrhizal roots

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Examination of the fossil roots of some of the earliest land plants has revealed the presence of vegetative fungal structures which are strikingly reminiscent of those found in present day vesicular-arbuscular (VA) mycorrhizas (Nicolson, 1975). Today, very few plants growing in natural plant communities are free from mycorrhizal infection. The presence of a supply of simple available carbon compounds either inside or close to the roots of autotrophic higher plants would clearly always have been a feature of great nutritional significance to heterotrophic micro-organisms the growth of which was otherwise limited in the soil environment, consisting as it does mostly of less-available carbon sources. If infection in turn provided the autotroph with improved access to minerals which were previously present in growth-limiting quantity, the vigour of both partners in a competitive situation would be improved. Such mutualistic associations were clearly favoured by selection pressures early in the colonisation of the terrestrial environment and they are now recognisable in the form of a number of distinctive root–fungus associations each characterised by a particular pattern of development and distribution of its vegetative mycelium and each most commonly, though not exclusively, associated with a particular complex of soil conditions and climate. Thus, those members of the Ericaceae which normally become dominant plants in acid mor-humus soils of cold sub-arctic and sub-alpine regions have a characteristic internal or endo-infection formed by ascomycetous fungi which is termed an 'ericoid' infection (Read, 1983). In contrast, on the mineral soils of higher pH, which occur in warmer and drier climates with high rates of organic matter turnover, grasses and herbs predominate and these mostly retain what may be regarded as the primitive VA type of infection caused by zygomycetous fungi of

genera such as *Glomus*, *Gigaspora* and *Acaulospora*. In this mycorrhizal type, in addition to a prominent internal phase consisting of vesicles for storage and arbuscules through which nutrient exchange with the host takes place, there is an important external mycelial phase.

Between the peaty heathland soils and the drier mineral soils of the grasslands lie the intermediate mor, moder and brown soils which frequently support forests. The dominant trees of these boreal and temperate forest zones – which are often members of the Pinaceae and Fagaceae in the northern hemisphere and of the Fagaceae and Myrtaceae in the southern hemisphere – have distinctive ecto- or sheathing mycorrhizas formed largely by Basidiomycetes, the vegetative mycelium of which is predominantly external, forming a compact sheath around the lateral roots and a more or less extensive mycelial phase in the surrounding soil. These broad relationships between environmental circumstances and mycorrhizal type are presented diagramatically in Fig. 1.

Since the mycorrhizal types can be seen to occupy specific positions along an environmental gradient of latitude and altitude it is logical to suppose that in each case their structure and function have evolved in response to the particular conditions of soil and climate prevailing at

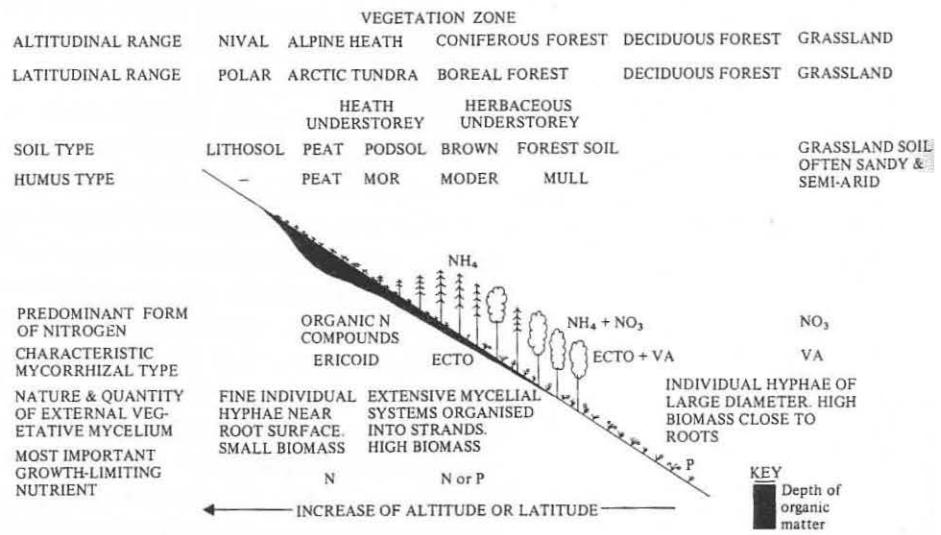

Fig. 1. Diagrammatic presentation of the postulated relationship between latitude or altitude, climate, soil and mycorrhizal type, and development of the vegetative mycelium associated with mycorrhizas.

that point on the gradient. As shown in Fig. 1 demarcation between zones is not always sharp, and intermediate areas occur in which plants bearing two types of mycorrhiza can grow together. Nonetheless the model provides a useful basis from which to analyse the relationship between structure and function of each mycelial type and the vegetation and soil type with which it is associated.

Distribution, structure and function of vegetative mycelium of ericoid mycorrhizas

Ericaceous species become dominant, and indeed often occur as the only plants, in heathland communities which dominate the cold and wet end of the environmental gradient (Fig. 1). Thus, they are best represented in the taiga zone around the northern polar ice cap and immediately below the nival zone in alpine areas. As a result of low soil temperatures, high rain or snowfall and low evaporation rates, soil moisture levels are high and decomposition and mineralisation processes are inhibited. Under these circumstances, organic matter accumulates to give deposits of peat or mor-humus to which the ericoid roots are largely restricted. The younger parts of these roots are devoid of root hairs but are themselves of very narrow dimensions and a dense fibrous root system is produced (Read, 1983).

The young cortical cells of these roots are filled with the much-branched vegetative mycelium of the ascomycetous fungus *Pezizella ericae* (Fig. 2). Examination of micrographs reveals that a very high proportion of the root biomass is made up of fungal material and that most of the vegetative mycelium is in the internal position (Fig. 2a,c). Careful analysis of the relative proportions of fungus to host material in each individual cell of such micrographs indicates that over 70% of the volume of the host cell is occupied by the fungus at the time when the infection unit is mature. The active life of each individual intracellular infection is of the order of four to five weeks and it is terminated by the breakdown of host cytoplasm which envelopes the internal mycelium in the healthy association (Duddridge & Read, 1982).

The external mycelium is relatively weakly developed (Fig. 2b). A very loose weft of hyphae is seen to cover the surface of the growing root and from this hyphae penetrate into each host cortical cell to form the individual infection units (Fig. 2c). Estimated numbers of entry points range from 250 to 2000 per cm of root in seedling roots of *Calluna vulgaris* (Read & Stribley, 1975). Surface views demonstrate clearly that most of the hyphae run parallel to the surface of the root and that some

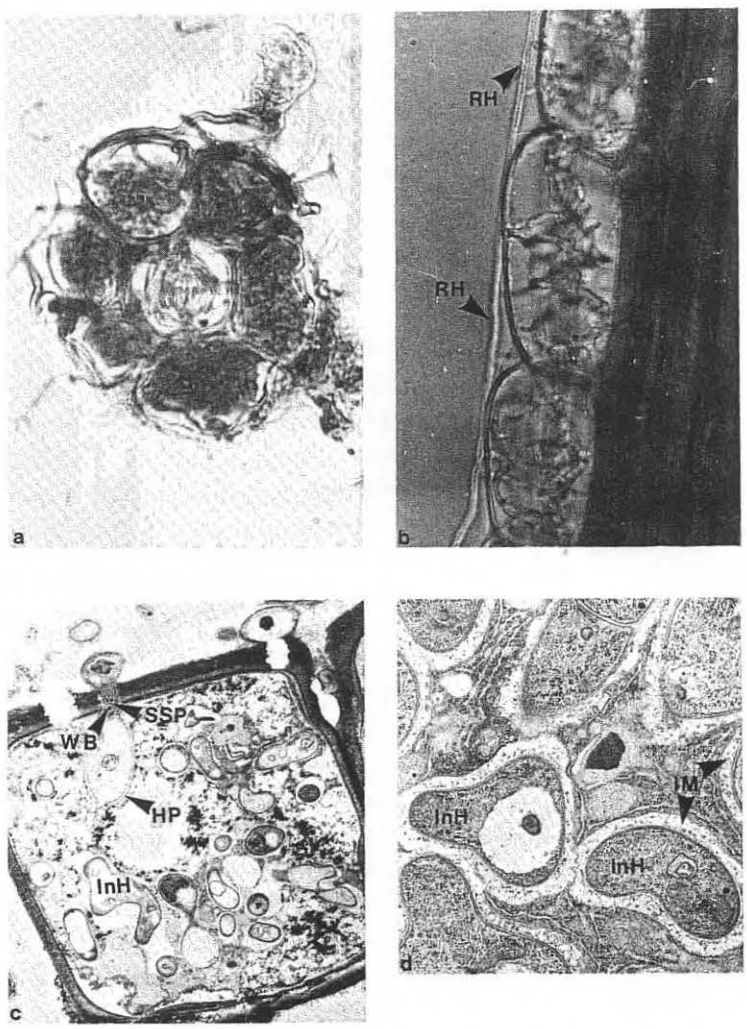

Fig. 2. (a) Transverse section of 'ericoid' root of *Calluna vulgaris* showing cortical cells filled with vegetative mycelium and the loose external weft of hyphae. × 800. (b) Early stage of infection of root of *Calluna vulgaris*. A 'runner' hypha (RH) growing parallel to the root surface produces lateral branches which penetrate the cortical cells and branch freely to produce the hyphal coils typical of ericoid infection. × 1000. (c) Transmission electron micrograph (TEM) of a root cortical cell of *Rhododendron ponticum* showing penetration of the cell wall by a hypha with simple septal pore (SSP) and Woronin body (WB) indicating ascomycetous affinities. Numerous internal hyphae (InH) can be seen surrounded by host plasmalemma (HP). × 2000. (d) High-magnification TEM of intracellular infection of the ericoid type.

of these which have rather larger diameters act as pioneers or runner hyphae from which lateral branches penetrate newly differentiated host cortical cells (Fig. 2b). Extension of mycelium outwards from the root surface is extremely restricted. It is difficult to obtain precise measurements of radial extension of hyphae in peat soils but recovery from sandy heathland soils can be relatively complete. In these circumstances hyphae normally penetrate little more than 1 cm from the root and the majority are restricted to the zone within 0.5 cm of its circumference. The external hyphae do not normally become organised into aggregates either on the surface of the root or in the surrounding soil. The effect of this distribution pattern is to produce a loose weft of mycelium around the root, the density of which is proportional to the intensity of internal infection. This weft is, however, never of a density comparable with that seen in ecto-mycorrhizas and, indeed, is not sufficient to form a complete cover over the surface of the root. The ratio of the biomass of external mycelium to that of internal mycelium is of the order of 0.1.

The predominantly internal development of the mycelium of ericoid mycorrhizas is probably of considerable significance from the functional point of view. In these systems the function of soil exploitation is to a large extent fulfilled by the diffuse and extensive 'hair-root' system. The colloidal organic matter into which the roots grow has a water-holding capacity so great that the roots are normally bathed in a dilute solution of carboxylic acids containing free and adsorbed nutrients. Under these circumstances investment of carbon in a large external network of hyphae would yield little advantage to the host.

Experiments on the endophyte in pure culture indicate that it may be relatively poorly adapted to outward extension into very acidic soil environments, since the optimum pH for growth is between 6 and 7 (Pearson & Read, 1975) and virtually no growth occurs between pH 3 and 4. The pH for optimal growth is thus closer to that of the vacuole of ericoid root cells than to that of heathland soils which are commonly in the range 3 to 4. This must be one of the reasons for the predominantly internal development of the fungus.

The mycorrhizal fungus is capable of producing acid-phosphatases, the level of activity of the enzyme being greatly stimulated at low

Caption for Fig. 2 (*cont.*)
A distinct electron-lucent zone, the inter-facial matrix (IM), surrounds all intracellular hyphae (InH). This zone forms a barrier across which all nutrient exchanges must take place and in which complexing of metallic elements is likely to occur. × 15 000.

external levels of inorganic phosphate (Pearson & Read, 1975). Organic phosphates, supplied in the form of ferric or aluminium inositol phytate are readily used as substrates for growth (Mitchell & Read, 1981). Organic nitrogen sources, in the form of amino acids, have been shown to be used as readily as ammonium by the endophyte in pure cultures (Pearson & Read, 1975) and later work (Stribley & Read, 1980) revealed that a range of amino acids could be used as nitrogen sources by mycorrhizal ericaceous plants whereas they were not readily used by the plants in the absence of the fungus. The mycorrhizal fungus thus provides the plant with a capacity to assimilate organic compounds of the kind which would be expected to be present in the colloidal matrix surrounding its roots.

A further attribute of the endophyte which may be of equal or greater importance to the host plant is its heavy-metal resistance. The solubility of potentially toxic metal elements such as aluminium, copper and zinc is greatly increased at the low pH levels prevailing in heathland soils and these elements pose a threat to the survival of plants under these circumstances (Rorison, 1973). Studies have revealed that the ericoid mycorrhizal fungus will grow in metal concentrations an order of magnitude greater than those survived by the host plant grown in the absence of the endophyte (Bradley *et al.*, 1982). It is likely that as shown in other fungi (Ashida, Higachi & Kikuchi, 1963; Paton & Budd, 1972; Duddridge & Wainwright, 1980) the resistance is based on the capacity of the fungus to complex metallic elements in its cell walls. The functional groups responsible for metal binding in the fungal cell wall are thought to be carboxylic-acid moieties of pectin-like substances (Tuominen, 1967). It is interesting that such substances are also present in quantity in the inter-facial matrix (Fig. 2d) between fungus and host cytoplasm in ericoid mycorrhizas (Duddridge & Read, 1982). The hyphal complexes within the host-cortical cell thus provide very large surface areas upon which metals can be complexed. These adsorption mechanisms lead to exclusion of metal ions from the shoot of the host plant which avoids the toxicity otherwise arising from their accumulation. In the absence of a mycorrhizal endophyte ericaceous plants have very little resistance to heavy metals which freely traverse the roots and accumulate in the shoots (Bradley *et al.*, 1981).

Distribution, structure and function of the vegetative mycelium of ectomycorrhizas

Environmental amelioration along the gradient in a southerly or downward direction arises through increasing mean summer temper-

atures and evapotranspiration rates. With an increased seasonality of climate and some surface drying of soil, coniferous trees replace ericaceous shrubs as dominants in the plant community though in the early part of the transition ericaceous shrubs, notably shade-tolerant members of the genus *Vaccinium*, continue to occur as dominants in the field layer. In contrast to the situation found in ericaceous plants, ectomycorrhizal conifers produce very large quantities of external mycelium, some of which is in the form of the sheath, the remainder being in the form of extensive fans of mycelium growing outwards from the sheath to exploit the soil over distances often in excess of 20 cm from the root (Skinner & Bowen, 1974*a*; Duddridge, Malibari & Read, 1980). Because of their delicacy these mycelial systems are normally broken when soil is excavated but analysis of their development is possible using root chambers with transparent walls (Brownlee, Duddridge, Malibari & Read, 1983) (Fig. 3a). In the case of *Suillus bovinus* mycelium associated with roots of *Pinus sylvestris* or *P. contorta*, the fans move through unsterile peat at rates of up to 3 mm day^{-1} in growth-chamber environments with temperatures of 20 °C day and 15 °C night. This may be compared with a growth rate of 7–8 mm day^{-1} recorded in the strand-forming wood decomposer *Serpula lacrimans* by Jennings (1982). In contrast to the mycelia of ericoid mycorrhizal systems, their growth is totally inhibited by waterlogging, indicating a sensitivity to anoxic conditions, and is generally in the direction of drier surface layers of the soil. This requirement for oxygen may be at least in part responsible for the exclusion of the ectomycorrhizal habit from the colder and wetter end of the gradient. Oxygen supplied as a result of internal transport from the air via plant intercellular spaces may be sufficient to initiate and sustain sheath formation (Read & Armstrong, 1972) but is unlikely to be sufficient to support outward growth of mycelium into the soil.

Hyphae within the mycelial fans often associate together to form more or less differentiated structures (Duddridge *et al.*, 1980) which have been variously described as 'strands', 'ropes' or 'cords'. These structures are not true rhizomorphs *sensu* Garrett (1956) since they lack a differentiated meristem and apical growth. Their structure and mode of growth is analogous to that seen in *Serpula lacrimans* (Falck, 1912; Butler, 1957).

Vessel hyphae of large internal diameter and generally lacking cytoplasm in the mature condition occupy the core of the strands (Duddridge *et al.*, 1980; Foster, 1981) and these are surrounded by densely cytoplasmic hyphae of smaller diameter. (Fig. 4 inset.)

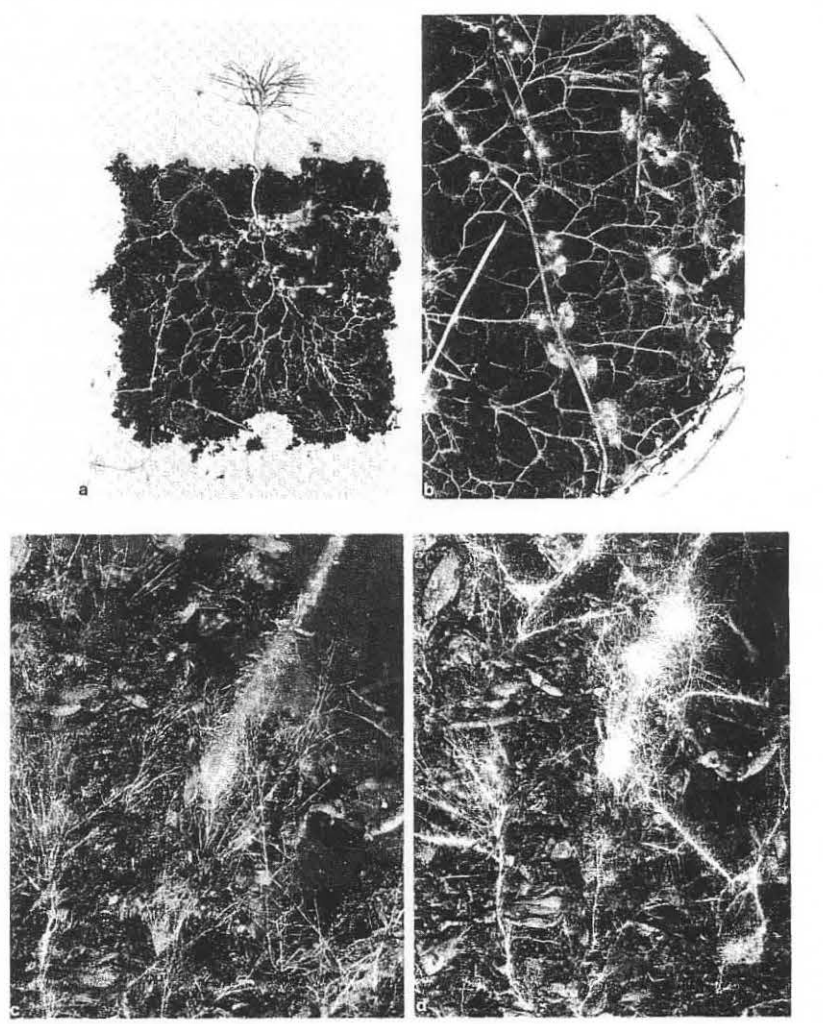

Fig. 3. (a) Seedling of *Pinus sylvestris* infected with the mycorrhizal fungus *Suillus bovinus* then grown for six weeks in unsterile peat in a transparent Perspex root chamber. Mycelial fans have developed from infected mycorrhizal laterals and exploited the peat throughout the chamber. × 0.2. (b) More detailed view of a similar mycorrhizal system showing the intensive exploitation of peat by mycorrhizal strands which arise from, and subsequently interconnect, mycorrhizal lateral roots. The actively-growing white primary root (left centre) alone remains infected. × 0.8. (c), (d) Sequential view of a growing lateral root of *Pinus contorta* as it comes into contact with advancing fans of *Suillus bovinus* mycelium in a root chamber. Figure 3c shows the root three days after contact with the hyphae. Some enhancement

Members of fungal genera such as *Suillus*, *Thelephora*, *Pisolithus* and *Lactarius*, which are among the commonest mycorrhizal associates of the Pinaceae, form particularly prolific differentiated fan systems of this kind. In the upper layers of soil under coniferous trees, the vegetative mycelium of these fungi probably represent by far the greatest component of microbial biomass clearly receiving an abundant supply of free carbon from the host to fuel its extension into the soil. It has even been suggested (Gadgil & Gadgil, 1971) that this growth is so vigorous that it leads to the competitive inhibition of decomposer organisms and reduction of decomposition rates, but this observation needs corroboration.

With further advance along the gradient of climate and soil, deciduous tree species become more important, members of the Fagaceae, notably *Quercus* and *Fagus*, dominating the ecosystem as conifers are excluded. Because of the relatively rapid rate of decomposition of the litter of these trees and of a higher base status of the leaves entering the litter, soil conditions under this type of vegetation are much ameliorated. Organic content and acidity are reduced and base status is increased. First moder and eventually brown forest soils with mull characteristics are encountered. The characteristic trees of such ecosystems are still ecto-mycorrhizal and some of their fungal associates, notably members of such genera as *Amanita* and *Lactarius* produce considerable quantities of external mycelium in addition to a sheath, but there is a trend towards decreased production of external mycelium along the gradient. In extreme cases, as in some beech forests, connections from sheath to the surrounding soil appear to be absent altogether (Harley, 1978). Clearly in such a circumstance the amount of vegetative mycelium in the soil will be much less than in the coniferous system and its function, assuming that one exists, might be quite different.

Since the pioneering work of Melin using pure culture syntheses of mycorrhizas we have known that one of the major functions of the external mycelium of coniferous roots is the absorption and translocation

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Caption for Fig. 3 (*cont.*)
of fungal growth is evident at the apex but the main root axis is uninfected and has root hairs. Little differentiation of the mycelium within the fans has occurred. Figure 3d shows the same root two weeks later. Infection has established at the root apex and arrested its extension, and two lateral roots behind the apex have also become infected. Following infection vigorous strand development occurs in some fans which are closely associated with the infected root. × 2.

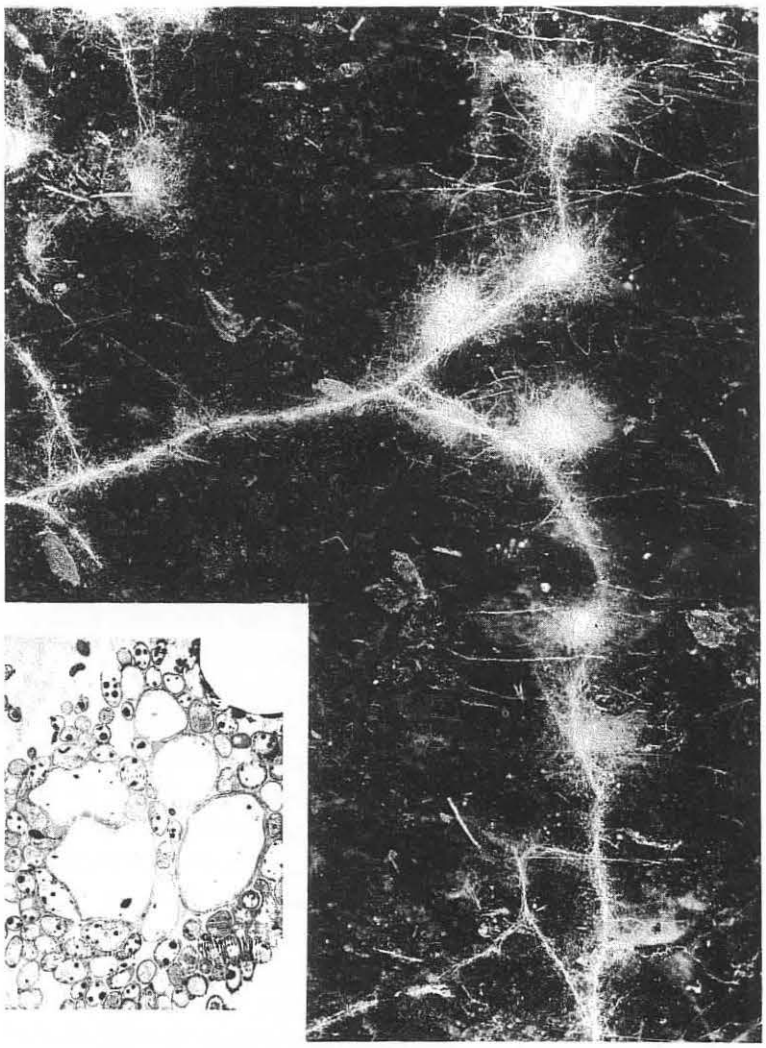

Fig. 4. Mature mycorrhizal roots of *Pinus contorta* infected with *Suillus bovinus*. The mycorrhizal laterals are interconnected by a single prominent strand while most of the diffuse hyphal network which makes up the fan of colonising systems has broken down. The outer surface of the strand is seen to be made up of loose hyphae which have intimate contact with the peat. × 50. (inset) TEM of transverse section through a mature strand of *Suillus bovinus* taken from a system similar to that shown in Fig. 4. Note differentiation into central, cytoplasm-free, vessel hyphae and loose surrounding densely-cytoplasmic sheath hyphae. × 1800.

of the major plant nutrients phosphorus (Melin & Nilsson, 1950) and nitrogen (Melin & Nilsson, 1952). Subsequent studies of detached roots of beech by Harley and his co-workers (Harley, 1969) have demonstrated that the ectomycorrhizal sheath is the site of exchange of phosphate absorbed from soil and of carbohydrates produced by the host. More recently attempts have been made in our laboratory to investigate the function of ecto-mycorrhizal mycelial systems again using observation chambers. Such chambers have the advantage that the normal source-sink relationship of the atmosphere-plant-mycorrhiza-soil pathway need not be broken even while direct visual, microscopic or experimental observations are being made. Examination of coniferous root systems in such chambers reveals that the roots occupy a comparatively small proportion of this soil in comparison with fungal mycelium which develops from its roots (Fig. 3b). In this case, therefore, in contrast to that seen in the ericoid root, the function of the roots appears to have been taken over by the fungus. One of the major functions of the mycelial fans, now demonstrated both in observation chambers (Brownlee *et al.*, 1983) and in the field (Fleming, 1983), is to act as inoculum which will infect roots either of the same plant, of another plant of the same species, or even, depending on the specificity of the fungus concerned, roots of other host species. Stages in the colonisation of an uninfected root after it has contacted a mycelial fan are shown in Fig. 3c,d. It can be observed that major strand development occurs only after contact with the root and the formation of mycorrhizas. Much of the rest of the fan system may subsequently break down leaving large strands connecting mycorrhizal roots (Fig. 4) and forming a potential supply line for compounds moving to or from, and between, roots (cf. Thompson, Chapter 9).

It has been shown experimentally that strands will absorb phosphorus and water from the soil and provide pathways for their transport to seedlings over considerable distances (Skinner & Bowen, 1974*a*,*b*; Duddridge *et al.*, 1980). Since this mycelial system anastomoses and connects a number of plants it follows that transport will be multi-directional probably along gradients of water potential, and that numerous plants interconnected by the same mycelial system can receive mineral nutrients and water absorbed by the fungus. If, as seems likely, most of the water and dissolved phosphate travel together, it will be through the vessel hyphae in the centre of the mycelial strands because their hydraulic conductivity will be much greater than that of the densely cytoplasmic hyphae which surround the vessels and make up the

rest of the mycelial fan. The ecological and physiological significance of these functional characteristics can be profound. Not only does the mycelial system provide a widely dispersed inoculum by which seedlings become infected early in their development, but the strands form

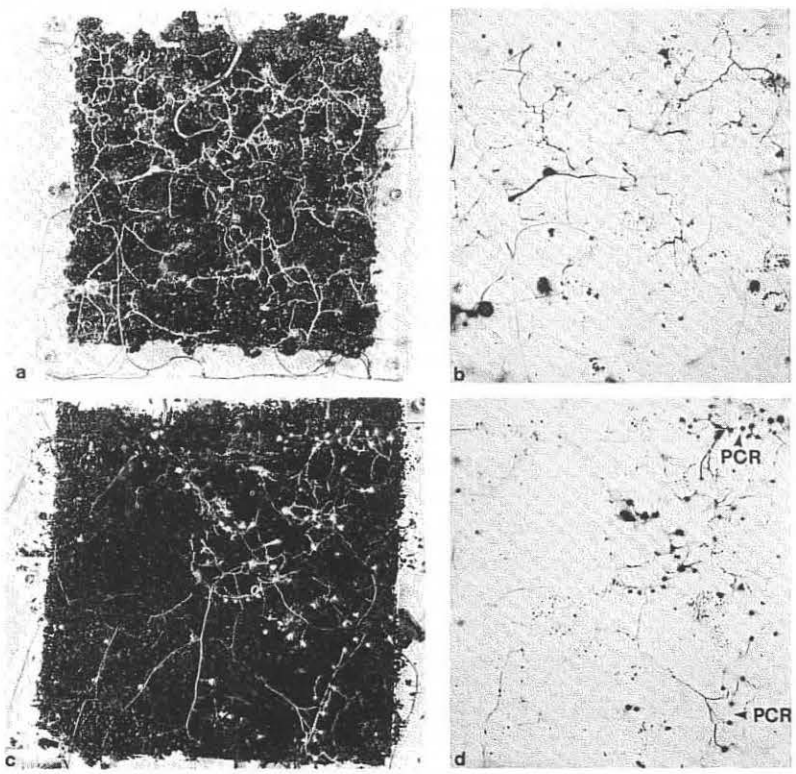

Fig. 5. (a) Roots and associated mycorrhizal mycelial system of a single seedling of *Pinus contorta* infected with *Suillus bovinus* in a root chamber. Most of the soil is exploited by mycelial strands. × 0.3. (b) Autoradiograph of chamber shown in Fig. 5a taken after exposure of the seedling shoot to $^{14}CO_2$ for 24 h and application of the film for a subsequent 24-h period. Note accumulation of label in clusters of mycorrhizal lateral roots and in the network of strands exploiting the peat. × 0.3. (c) Roots and associated mycorrhizal mycelial system of an interspecific association of host seedlings of *Pinus sylvestris* (left) and *P. controta* (right) in which an infection initiated on *P. sylvestris* by *Suillus bovinus* has spread to a younger *P. contorta* seedling. × 0.3. (d) Autoradiograph of the interspecific association shown in Fig. 5c taken after feeding the *P. sylvestris* shoot with 14_{CO_2} for 24 h. Extensive transfer of labelled assimilate has occurred to mycorrhizal laterals on the roots of *P. contorta* (PCR).

functional connections through which seedlings can be supplied with nutrients and water during the critical establishment phase.

The importance of carbon transfer to developing seedlings must also not be underestimated. Autoradiographic analyses of mycelial systems after the application of $^{14}CO_2$ to a single seedling shoot, reveal that current assimilate accumulates in the mycorrhizal roots and from these moves rapidly outwards into the external network of hyphae (Fig. 5a,b). Assimilate moves to the edge of the growing fan in developing systems but in cases wh :ctions between plants have developed (Fig. 5c) label accumulates in the mycorrhizal roots of 'receiver' plants (Fig. 5d). Such transfer occurs in both intra- and inter-specific combinations of host plants. In order to sustain an efficient mycorrhizal system an isolated seedling would have to invest significant quantities of carbon in the fungus. If the carbon can, as appears likely, be supplied from alternative sources such as more mature seedlings through fungal mycelia this burden is reduced or eliminated. Thus the seedling, which may often in a forest environment be growing in deep shade, might become relatively independent of photosynthate from its own shoots and is supported by transfer of assimilates produced in the relatively well-illuminated crowns of over-story trees. Seen from this point of view the vegetative mycelium of ecto-mycorrhizas is of critical importance not only for the survival of seedlings but for the whole process of nutrient cycling in forest ecosystems.

It is important to recall, however, that some ectomycorrhizal systems – like those in many beech forests, while having thick sheaths do not produce the extensive mycelial phase in the soil (Harley, 1978). The ecological significance of mycorrhizal roots which are not connected to the surrounding soil by hyphae must be re-assessed. A clue to the differences in structure and function between the two types may come from study of the soil. Litter added to the mor-humus soil of coniferous forest breaks down slowly through the growing season and in these circumstances it may be necessary for absorptive fungal surfaces to be in close proximity to the sites of release if nutrients are not to be lost to competing saprotrophic fungi. Nutrient release from deciduous leaves like beech is, in contrast, a relatively rapid process. Whereas only 1–2% of the dry weight of newly fallen spruce needles can be leached by water, the value for litter of deciduous trees is nearer 20% (Nykvist, 1963). A capacity for efficient absorption at the time of the 'flush' of nutrient release coupled with a storage function would here be an advantage while the maintenance of an extensive mycelial system in the

soil throughout the growing season would be wasteful of resources. The racemosely branched mycorrhizal roots of beech form a layer immediately below the recently fallen litter where their thick sheaths are in an ideal position to absorb nutrients leached from above.

The fungi of ectomycorrhizal beech roots produce large quantities of surface-bound phosphatases and the activity of these enzymes is many times greater in infected than in uninfected roots (Williams & Alexander, 1975). Bartlett & Lewis (1973) showed that the phosphatase hydrolysed a number of organic and inorganic phosphates, the released orthophosphate being absorbed by the sheath. The phosphate-storage capacity of the sheath is large and estimates suggest that in beech, absorption rates of phosphate are five times greater in mycorrhizal than in non-mycorrhizal roots, on an area basis, and over twice as great on a mass basis (Harley & McCready, 1950). Similar results have been obtained with pine (Bowen & Theodoru, 1967). Phosphate is stored in the fungal sheath in the form of polyphosphate granules. Using histochemical staining techniques Chilvers & Harley (1980) showed that P accumulation was accompanied by deposition of these granules in the sheath and that the number of granules produced approximately paralleled the rate of phosphate uptake. More recently Harley & McCready (1981) have demonstrated that with low levels of external phosphate, similar to those found in the field, about 40% of the total absorbed P is converted into polyphosphate. At higher concentrations such as those which might prevail for short periods during seasonal flushes of nutrient release, up to 97% of P storage may be in the form of polyphosphate. Over subsequent periods of time, granule numbers in the sheath decline; this suggests that the phosphate is being mobilised and passed into root tissue. While most of the research emphasis to date has been devoted to beech it seems likely that the same pattern of phosphate storage and release is found in all ectomycorrhizal species. The major distinctions within these mycorrhizal systems thus involve differences in mode of nutrient capture and these in turn are determined by the physicochemical characteristics of the resource material. Scavenging by an extensive mycelial network is a feature of slow-release situations such as those found in mor-humus soils dominated by pine while efficient absorption and retention without extensive hyphal ramification beyond the sheath is a feature of environments with pronounced nutrient flushes such as are found in moder and brown forest soils under deciduous species.

The direction of flow of water and of its dissolved nutrients is probably governed by a simple source-sink relationship in which the

major determining factor will be the transpiration flux from the host shoot. Under most environmental circumstances the fall in water potential at the leaf-air interface will be greater than at any other part of the pathway so water will move to the tree, which is also the food base. The densely-cytoplasmic mycorrhizal sheath might be expected to impose a significant resistance to flow in the pathway but calculations have shown that its hydraulic conductivity is large and that it imposes no significant impedance to flow (Sands *et al.*, 1982). Both the direction of water flow and the driving mechanism appear to be distinct from that observed in the saprotrophic strand-forming fungus *Serpula lacrimans* in which water moves away from the food base towards the growing hyphal front along a gradient of hydrostatic pressure generated by high internal solute concentrations (Jennings, Chapter 7).

The direction and mechanism of assimilate transfer may, on the other hand, be very similar in the two fungal systems. While water and mineral nutrients travel towards the autotroph in the mycorrhizal system, carbon flows in the opposite direction. In the case of *Serpula* also, assimilates move from food base to the growing hyphal front (Jennings, 1982) and we may assume that in both systems some of these are used for construction of new hyphal walls, thus maintaining a concentration gradient. It is interesting that the major compound involved in the assimilate flux in strands of ectomycorrhizal mycelium is trehalose (D. J. Read, unpublished), which suggests that in qualitative terms also, the assimilate transport system is similar to that occurring in *Serpula* (Jennings, Chapter 7).

Since bidirectional flow must occur in the strands of ectomycorrhizal mycelium it has been proposed (Brownlee *et al.*, 1983) that the transport system is both structurally and functionally analogous to that found in the plant. Water and dissolved salts move towards the transpiring surface through vessel hyphae of large diameter which lack cytoplasm and are thus comparable with xylem vessels, while assimilates move towards the hyphal front through the cytoplasmic hyphae surrounding the vessels which are thus analogous to sieve tubes. Evidence to support this hypothesis is currently being sought using micro-autoradiographic techniques.

Distribution, structure and function of the vegetative mycelium of VA systems

VA mycorrhizas become dominant in plants at the warmer and drier end of the environmental gradient. As in the case of the heath-forest boundary, however, there is again an overlap in that the forest

floor vegetation of the more base-rich coniferous forests and of most deciduous forests consists of herbs with VA mycorrhizal infection. Climatic conditions in areas supporting VA mycorrhizal plants as dominants are such that turnover of organic matter is rapid and evaporation rates are high. This leads to a net upward movement of salts, replacing the leaching tendency experienced in upper and most intermediate parts of the gradient and leading to a higher pH. Grasslands often form the characteristic vegetation in such areas, the dominant graminaceous plants occurring in mixture with herbs and occasional shrubs. Practically all plants in such associations have VA mycorrhizas though members of some plant families like the Cruciferae, Polygonaceae, Juncaceae and Cyperaceae are normally free of this type of infection. The quantity of external mycelium varies as in the case of ectomycorrhizas with soil type and host, and though it does not reach the levels either in terms of biomass or differentiation seen in the ectomycorrhizas of coniferous mor-humus soil it can, nonetheless, form an extensive network. Nicolson (1959) observed particularly extensive wefts of external mycelium around heavily infected roots of grasses in stabilised parts of sand dunes. Estimates of hyphal length vary between 0.8 and 1.3 m per cm infected root (Sanders, Tinker, Black & Palmerley, 1977) and lengths of up to 55 m have been recorded per gram of soil associated with roots in grassland (Tisdall & Oades, 1979). Such a network must clearly represent a large increase in the potential absorptive surface of the root. The hyphae making up the external mycelium have distinctive forms and dimensions. There is a striking variation in diameter from 2 to 30 μm accompanied by great variation in wall thickness. In mature mycelial systems, thick-walled hyphae normally of diameters between 20 and 30 μm give permanence to the external mycelial complex. These have characteristic elbow-like bends which were first described by Peyronel (1924), and termed angular-projections by Butler (1939). Finer thick-walled hyphae branch from these and the ultimate branches are relatively ephemeral thin-walled structures with a diameter of 2–7 μm. Mosse (1959) reported that 75% of the external hyphae associated with apple roots were of the coarse type, in this case with a diameter up to 20 μm. From the external mycelium lateral branches, often formed at right angles to the main hyphae and running in parallel to the roots as in ericaceous mycorrhizas, penetrate the outer cortical cells of the root. The number of entry points varies between 2.6 and 21.1 mm^{-1} of root length in strawberry, and between 4.6 and 10.7 in apple (Mosse, 1959). Internally the mycelium differentiates into vesicles

(Fig. 6a) which are largely filled with lipid reserves (Cooper & Lösel, 1978) and finely divided intracellular arbuscules (Fig. 6b) each branch of which is closely enveloped in host-plasmalemma.

Aspects of the physiology of VA mycorrhizas have been reviewed recently (Gianinazzi-Pearson & Gianinazzi, 1983), and only the function of the vegetative mycelium will be examined here. The evidence indicates that fungal enhancement of phosphorus uptake is the main reason for improvement of growth and yield in VA mycorrhizal plants. As in ecto-mycorrhizal systems, infected roots can absorb significantly more phosphate from culture solutions (Gray & Gerdemann, 1969) and from soils (Mosse *et al.*, 1973; Sanders & Tinker 1973; Gianinazzi-Pearson, Fardceau, Asimi & Gianinazzi, 1981) than uninfected roots. This difference is particularly well marked when levels of available P are low enough to limit growth. The VA mycorrhizal root system has a higher affinity for phosphate ions than the uninfected root (Cress, Throneberry & Lindsey, 1979) which in turn leads to significantly greater P inflow rates (Sanders & Tinker, 1973; Smith, Nicholas & Smith, 1979; Smith, 1982) and the vegetative mycelium extending outwards into the soil is known to be the major absorbing surface (Hattingh, Gray & Gerdemann, 1973; Pearson & Tinker, 1975; Cooper & Tinker 1978).

Once absorbed, phosphate is translocated through VA hyphae at rates calculated to be in the range $0.1–3.8 \times 10^{-9}$ mol. cm s^{-1} (Sanders & Tinker 1973; Pearson & Tinker, 1975). Tinker (1975) has proposed that the transport mechanism involves a combination of bulk flow and cytoplasmic streaming, the concentrations of P in the hyphal cytoplasm being regulated by loading or unloading of polyphosphate (poly P) in vacuoles. As in ectomycorrhizas the presence of poly P granules in the fungal vacuoles has been confirmed by electron microscopy (Cox, Sanders, Tinker & Wild, 1975; White & Brown, 1979; Strullu, Gourret, Garrec & Fourcy, 1981*a*; Strullu, Gourret & Garrec, 1981*b*). Again as in ectomycorrhizas, it has been shown that poly P rapidly accumulates in the external hyphae of P-starved mycorrhizal plants which are supplied with orthophosphate and that as much as 40% of the fungal P may be stored in the form of poly P in the hyphal vacuoles (Callow, Capaccio, Parish & Tinker, 1978). The arrival of this polyphosphate in the internal mycelium is associated with an increase of polyphosphate kinase activity and this activity appears to be restricted to the internal phase of fungal growth (Capaccio & Callow, 1982). Polyphosphate granules disappear from the vacuoles in the fine arbuscule branches (Cox *et al.*, 1975; Strullu *et al.*, 1981*b*) and it seems likely that the

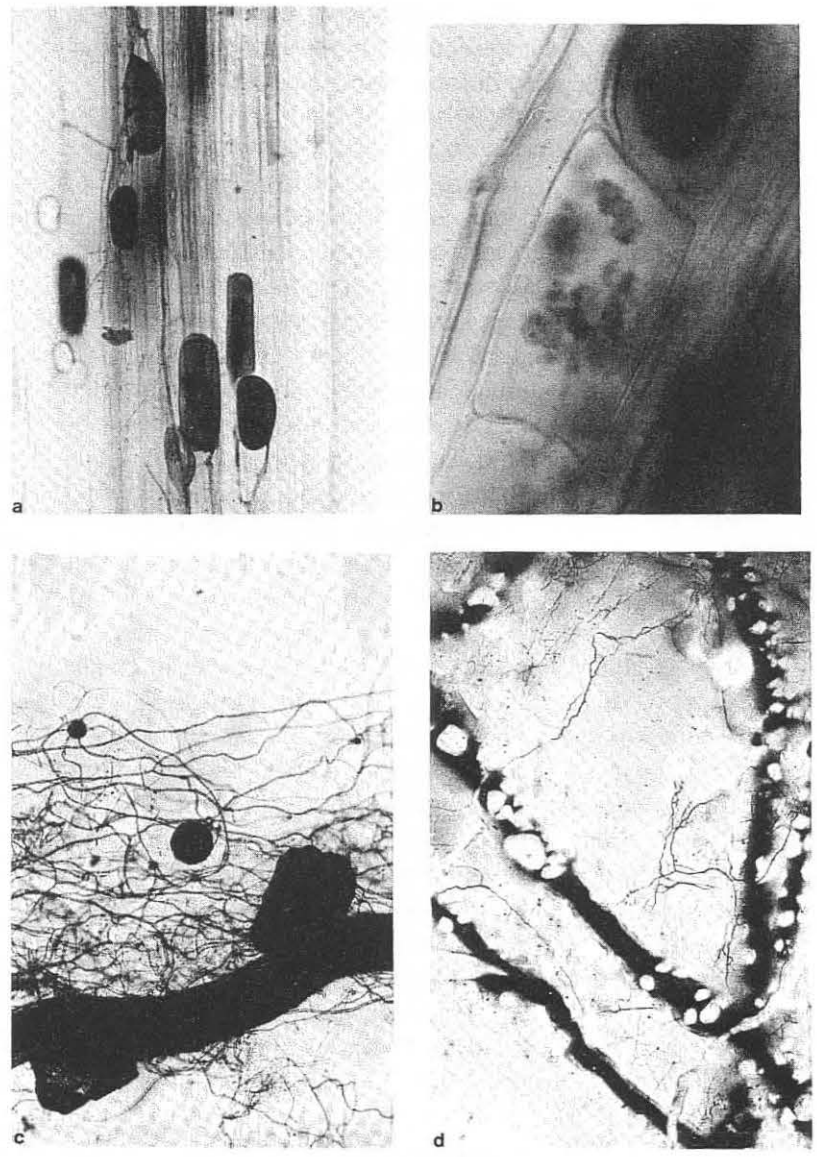

Fig. 6. (a) Vesicles of the VA mycorrhizal fungus *Glomus tenue* in cortical cells of the roots of *Festuca ovina*. × 100. (b) Arbuscule of a VA mycorrhizal fungus in root cortical cell of *Festuca ovina*. × 300. (c) Vegetative mycelium and chlamydospores of the VA mycorrhizal fungus *Glomus clarum* infecting lateral roots of *Festuca ovina* growing in dune-sand. Plants were inoculated with spores of the fungus and grown for six weeks before the soil was gently removed under a slow

released orthophosphate is actively transported from fungus to host across the interface between the arbuscule and the host plasmalemma (Cox & Tinker, 1976). Marx, Dexheimer, Gianinazzi-Pearson & Gianinazzi (1982) have shown that ATPase activity associated with the host plasmalemma is concentrated around the fine branches of the arbuscular hyphae.

In addition to the well established role of the mycorrhizal mycelium in absorption and transfer of phosphorus, interest is increasingly being devoted to its rôle in uptake of water (Safir, Boyer & Gerdemann, 1972; Allen, Smith, Moore & Christensen, 1981; Allen 1982; Hardie & Leyton, 1981) and trace elements (Lambert, Baker & Cole, 1979). On theoretical grounds, if mycorrhizal enhancement of nutrient uptake occurs as a result of the capacity of the external mycelium to exploit larger volumes of soil then plant growth response should increase in proportion to the quantity of external mycelium produced. Evidence that this is the case has now been obtained in studies employing a range of endophytes and host species (Saunders *et al.*, 1977; Graham, Lindermann & Menge, 1982).

It is now realised that as well as playing a fundamental role in plant nutrition, the external mycelium of VA mycorrhizas in natural vegetation systems is more important than spores as a source of inoculum (Read, Koucheki & Hodgson, 1976). The implication of this observation is the same as that made in the ectomycorrhizas, namely that for a period after infection of a root has taken place, the vegetative mycelium forms a direct interconnection between the infected plants. The external mycelium of VA mycorrhizas is less structurally differentiated (Fig. 6c) than that of ectomycorrhizas which makes it more difficult to examine the function of these interconnections experimentally. However, a number of studies have shown that phosphorus may be transferred either directly or indirectly from plant to plant through VA hyphae (Heap & Newman, 1980; Chiariello, Hickman & Mooney, 1982; Whittingham & Read, 1982). It has been shown also that the flux of nutrients from source to sink plants can be sufficient to promote growth

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Caption for Fig. 6 (*cont.*)
jet of water. Note the extensive, but largely undifferentiated, external mycelium. × 50. (d) Autoradiograph of a similar root system after feeding the host shoot with $^{14}CO_2$. Note extensive transfer of label from roots to external vegetative mycelium. White patches on roots are caused by adhering sand grains which interrupt isotope emission. × 50.

responses of the sinks (Whittingham & Read, 1982). As in the ectomycorrhizas, transfer of carbon from source plants to sink seedlings at both the intra and interspecific levels have been demonstrated (Francis & Read, 1984). This transfer is greatly enhanced if sink seedlings are shaded, indicating again that in the natural environment inter-plant mycelial connections may provide direct channels of support for seedlings in the critical establishment phases. Preliminary evidence that the transfer of carbon is by the direct mycelial pathway rather than by leakage of assimilates from the root of source plants and later absorption by scavenging hyphae is now available in the form of autoradiographs (Fig. 6d) showing labelled hyphal 'bridges' between roots (Francis & Read, 1984).

The occurrence of the VA mycorrhizal type at the warm, dry end of the environmental gradient is probably of importance in a functional sense. Under the circumstances of high turnover of nutrients which prevail in such a climate, plant growth is potentially rapid at least after periods of rain, but may be limited by the levels of availability of the least-mobile nutrient elements. Because of its strong affinity with adsorption sites in soil minerals, phosphorus is frequently the element which most limits growth in mineral soils (Tinker, 1975, 1978; Gianinazzi-Pearson & Diem, 1982), and zones of P depletion are known to occur around growing roots (Nye & Tinker, 1977). Clearly any structure which has the capacity to grow through and beyond such depletion zones has the potential to remove the growth limitations and would provide the plant with considerable competitive advantage. Baylis (1975) has proposed that selection pressures in nutrient-deficient habitats have led to the evolution of two major alternative strategies for nutrient capture in nature. Both provide the plant with the capacity to 'forage' for nutrients like phosphorus beyond the depletion zone. In the first, plants invest carbon in the production of a diffuse root system with extensive root-hair development; in the second, carbon is invested in a mycorrhizal fungus the external mycelium of which has the function of soil exploitation. In the latter type root hairs may be totally lacking and plants are obligately mycorrhizal. The two distinct strategies have been observed in plants of tropical rain forests (St John, 1980). Many plants, for example some members of the Gramineae, appear to occupy an intermediate position having both a diffuse root system with root hairs, and extensive VA infection. It is difficult to envisage what nutritional advantage the mature plant may gain from mycorrhizal infection in such conditions though infection in the seedling stage, as indicated earlier,

may be of great significance, and retention of infection would maintain the integration of the population of mycorrhizal plants so that nutrients can move from areas of relatively good to areas of relatively weak supply thus maintaining vigour at the community rather than at the individual level.

General discussion

It is almost one hundred years since Frank (1885) provided the first description of a root-fungus association which he termed a mycorrhiza in the Cupuliferae. Since this time we have made considerable advances in our understanding of this symbiosis. The early studies typified by those of Melin (1923) and Hatch & Doak (1933) on ectomycorrhizas, and Gallaud (1905) and Peyronel (1924) on VA mycorrhizas, placed major emphasis on description of the structural features of the associations. Later, vital information on their function was obtained using aseptic synthesis techniques (Melin & Nilsson, 1950, 1952, 1953), field and pot culture studies (Hatch, 1937), and laboratory analytical procedures with detached roots (Harley, 1969; Harley & Smith, 1983). These and other similar studies have laid the basis for an understanding of mycorrhizal structure and function at the level of the individual plant or root. As a result of these pioneering studies we are now in a position to ask questions about the role of mycorrhizas in plant communities and ecosystems. Such enquiries promise to bring exciting developments. It is increasingly apparent that many plants in both ectomycorrhizal and VA mycorrhizal associations are interlinked by the vegetative mycelium of their fungal associates. The general lack of host specificity shown by mycorrhizal fungi means that these interconnections can occur at both the intra- and interspecific level throughout the plant community. The implication of the existence of such functional pathways for subjects such as nutrient cycling, seedling establishment and competition between plants both at the individual plant and community level are profound and further emphasis on this area of research is greatly needed. The biology of the vegetative mycelium of mycorrhizas must become a subject of research not only for mycologists but for all those who wish to obtain a full understanding of the dynamics of terrestrial ecosystems.

I thank the NERC, the SERC and the Forestry Commission for financial support. Thanks are also due to Mr G. Woods and Mr D. Hollingworth for photographic assistance, to Dr C. Brownlee, Dr J.

Duddridge and Mr R. Francis for providing some previously unpublished photographs, and to Miss J. Bird for patiently typing the manuscript.

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